Supplementary Information Evolutionary History of Modern Samoans

Authors: Daniel N. Harris[1,2,3], Michael D. Kessler[1,2,3], Amol C. Shetty[1,2,3], Daniel E. Weeks[4,5], Ryan L. Minster[4], Sharon Browning[6], Ethan E. Cochrane[7], Ranjan Deka[8], Nicola L. Hawley[9], Muagututi'a Sefuiva Reupena[10], Take Naseri[11], Trans-Omics for Precision Medicine (TOPMed) Consortium, TOPMed Population Genetics Working Group, Stephen T. McGarvey[12,13], and Timothy D. O'Connor[1,2,3*]

Supplementary Text

Supplementary Text 1. Papuans introduced Denisovan ancestry into Remote Oceania

Papuan populations have the largest proportion of Denisovan ancestry of any studied human population (1), and the introgression of this ancestry is estimated to have occurred approximately 44,000 years ago (2). Therefore, we hypothesize that it is likely that Papuan admixture introduced Denisovan haplotypes into Samoans and other Austronesian groups (3). Due to the recent divergence between East Asian and Austronesian populations, and the low level of Denisovan ancestry in East Asian populations (1, 4, 5), we utilize the Han Chinese in our D statistic (i.e. D(Chimpanzee,Denisovan;Han,X)) as the alternative population to test for the presence of Denisovan ancestry in Samoa. Therefore, any tests identifying a Denisovan admixture signal indicate the gene flow occurred after the divergence of East Asians and Austronesians (Figure 2). In support of our hypothesis, we find a strong correlation between an Austronesian individual's Papuan ancestry proportion and their D-statistic test for Denisovan ancestry, after controlling for Neanderthal ancestry ($P_{Den} < 2x10^{-16}$, $\beta_{Den}=18.654$, Figure 2). However, we find no corresponding correlation with Neanderthal ancestry ($P_{Nea} = 0.981$). These results suggest that the Denisovan ancestry in Samoans and other Austronesians arrived through Papuan admixture in Oceania, which is consistent with Reich*, et al.* (3), and might even be impacting Austronesian phenotypes. Due to the large sample size of our Samoan dataset and their extensive phenotypic profiles (6), these Samoan individuals represent an excellent cohort to further study Denisovan admixture and its potential impact on modern human phenotypes (7).

Supplementary Text 2. Greater Admixture and Genetic Diversity in Urban Regions

The large sample size and dense geographic sampling of Samoans in this study gives us the statistical power to examine differences in the admixture histories between the two main Samoan islands. We find that the AUA census region has the greatest amount of admixture from non-Samoan sources, followed by NWU, ROU, and SAV (Figure S8), and is consistent with the urban regions (AUA and NWU) being the main locations of European and East Asian migration and introgression (8, 9). Furthermore, this pattern of greater admixture in urban areas is observed in other global areas with histories of European colonization (10). Interestingly, the NWU region has the most East Asian admixture while AUA has the most European and African ancestry (Figure S8).

The average number of heterozygous sites is greatest in the urban regions, and greater on Upolu than on Savai'i. However, this pattern is eliminated when admixed samples are removed from the analysis, which results in SAV and NWU having the greatest heterozygosity (Table S3), and supports the idea that admixture greatly impacts heterozygosity patterns between census regions. Singleton variant patterns are similar to those seen across heterozygous sites, except that singleton patterns are relatively similar in admixed and non-admixed individuals (Table S4). Given the young age of singletons, this suggests that recent changes have led to Upolu having greater genetic diversity than Savai'i. This also indicates that Apia was the main population center of Samoa prior to European arrival, since the difference in singletons is not entirely driven by admixture. However, European admixture is still likely to be a contributor to this difference in genetic diversity, since the differences in singleton totals between regions is greater when admixed samples are included in the analysis.

Supplementary Tables and Figures:

Table S1. Reference population sample size and general location from Lazaridis, *et al.* (11) and Pugach, *et al.* (12). All non-Oceanic populations are grouped into their main continental region. Polynesian and Polynesian Outliers are a sub-classification of the Austronesian ancestral source.

Population	Sample Size	Country	Ancestral Source
African	309	NA	NA
Caucasus	52	NA	NA
CentralAsian/Siberian	244	NA	NA
East Asian	274	NA	NA
European	537	NA	NA
Middle Eastern	187	NA	NA
Native American	77	NA	NA
South Asian	262	NA	NA
Australian	2	Australia	Australian
Australian_WGA	5	Australia	Australian
Borneo	9	Indonesia	Austronesian
Semende	8	Indonesia	Austronesian
Buka	7	Papua New Guinea	Austronesian
Kove	8	Papua New Guinea	Austronesian
Lavongai	15	Papua New Guinea	Austronesian
Madak	8	Papua New Guinea	Austronesian
Mamusi	13	Papua New Guinea	Austronesian
Mamusi_Paleabu	5	Papua New Guinea	Austronesian
Mangseng	5	Papua New Guinea	Austronesian
Manus	2	Papua New Guinea	Austronesian
Melamela	6	Papua New Guinea	Austronesian
Mengen	9	Papua New Guinea	Austronesian
Mussau	10	Papua New Guinea	Austronesian
Nailik	7	Papua New Guinea	Austronesian
Nakanai_Bileki	5	Papua New Guinea	Austronesian
Nakanai_Loso	5	Papua New Guinea	Austronesian
Notsi	7	Papua New Guinea	Austronesian
Saposa	8	Papua New Guinea	Austronesian
Teop	7	Papua New Guinea	Austronesian
Tigak	7	Papua New Guinea	Austronesian
Tolai	18	Papua New Guinea	Austronesian
Mamanwa	9	Philippines	Austronesian
Mamanwa1	5	Philippines	Austronesian
Choiseul	7	Solomon Islands	Austronesian
Gela	6	Solomon Islands	Austronesian
Isabel	7	Solomon Islands	Austronesian

Kolombangara	4	Solomon Islands	Austronesian
Makira	6	Solomon Islands	Austronesian
Malaita	6	Solomon Islands	Austronesian
Ranongga	6	Solomon Islands	Austronesian
Santa_Cruz	7	Solomon Islands	Austronesian
Ontong_Java	7	Solomon Islands	Polynesian Outliers
RenBel	7	Solomon Islands	Polynesian Outliers
Tikopia	6	Solomon Islands	Polynesian Outliers
Tongan	6	Tonga	Polynesian
Ata	7	Papua New Guinea	Papuan
Baining_Malasait	4	Papua New Guinea	Papuan
Baining_Marabu	8	Papua New Guinea	Papuan
Bougainville_South	2	Papua New Guinea	Papuan
Kol_New_Britain	2	Papua New Guinea	Papuan
Kuot_Kabil	5	Papua New Guinea	Papuan
Kuot_Lamalaua	4	Papua New Guinea	Papuan
Nasioi	10	Papua New Guinea	Papuan
New_Guinea	19	Papua New Guinea	Papuan
Papuan_1	14	Papua New Guinea	Papuan
Papuan_2	4	Papua New Guinea	Papuan
Papuan_Central	5	Papua New Guinea	Papuan
Papuan_Gulf	3	Papua New Guinea	Papuan
Sulka	14	Papua New Guinea	Papuan
Russell	3	Solomon Islands	Papuan
Savo	7	Solomon Islands	Papuan
Vella_Lavella	6	Solomon Islands	Papuan

Table S2. D-statistic of the form D(Yoruba, Papuan Source, Han, Samoan) tests for the presence of Papuan admixture in Samoans from five different Papuan populations.

Papuan Source	**D**	**SE**	**Z**
New_Guinea	0.0575	0.001782	32.284
Papuan_2	0.0582	0.001897	30.668
Papuan_1	0.0585	0.001768	33.081
Baining Malasait	0.0617	0.001875	32.889
Baining Marabu	0.0620	0.001869	33.160

Table S3. Average heterozygosity (Het.) per census region of all unrelated Samoans (ALL) and unrelated Samoans with 99% of their genome attributed to the Austronesian ADMIXTURE cluster (Filter), with standard error calculations (SE) and sample size.

Census Region	ALL Sample Size	ALL Het.	ALL SE	Filter Sample Size	Filter Het.	Filter SE
AUA	230	1,787,773.448	5,677.745	76	1,728,183.776	1,008.128
NWU	285	1,768,880.326	3,081.174	102	1,730,624.500	993.036
ROU	258	1,761,150.329	3,039.890	121	1,727,320.545	1,074.581
SAV	196	1,751,132.362	2,984.276	120	1,728,266.267	13,38.879

Table S4. Average number of singletons (Sing.) per census region of all unrelated Samoans (ALL) and unrelated Samoans with 99% of their genome attributed to the Austronesian ADMIXTURE cluster (Filter), with standard error calculations (SE) and sample size.

Census Region	ALL Sample Size	ALL Sing.	ALL SE	Filter Sample Size	Filter Sing.	Filter SE
AUA	230	8,512.670	1,078.854	76	2,114.289	20.027
NWU	285	5,616.568	299.840	102	2,081.618	17.468
ROU	258	5,396.903	378.417	121	2,058.421	18.105
SAV	196	4,139.189	336.662	120	1,938.675	23.526

Table S5. Samoan archaeological record and other historical events. The icons correspond to those in Figure 4 plus some additional time points of interest.

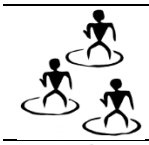
Icon	Event	Date (years ago)
	Upolu island settled by people with Lapita pottery (13-15).	2,750-2,880
	Remaining islands sparsely settled by relatively isolated populations with plainware pottery (16-21).	2,100-2,700
	Possible migration of population(s) into Samoa from the west, likely through the Micronesian Caroline islands (17).	1,500-2,000
	Pottery disappears (22, 23).	1,000-1,500
	Tutuila volcanic activity including 20 cm thick ashfall on Tafuna plain (24, 25).	1,300-1,400
	Inter-archipelago voyaging increases dramatically with Samoan basalt artifacts found across the central Pacific; East Polynesia colonized from Samoa and Tonga (19, 26, 27).	800-1,000
	The fast rise of regionalized Samoan chiefdoms, Larger coastal villages, monumental stone/earth mounds, inland fortified settlements, landscape modifications including terraces and agricultural infrastructure originate. (23, 28).	500-1,000
	Traditional history records Tongan incursions into Samoa, coeval with the developing Tongan Maritime chiefdom.	850
	Arrival of missionaries and sustained contact with Europeans, population concentrated in coastal areas; periods of massive population decline caused by European disease.	230

Figure S1. Map of islands in Near Oceania and Remote Oceania.

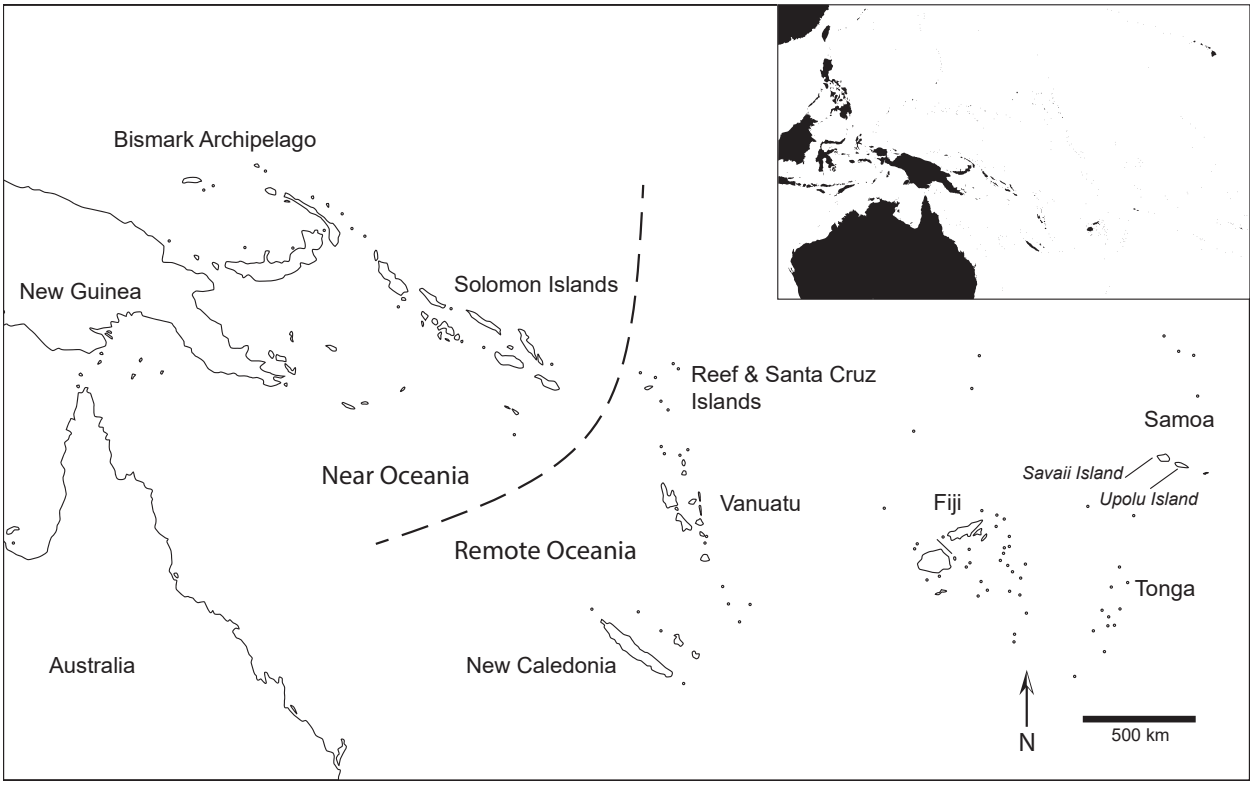


Figure S2. Map of the Samoan sampling locations with topographic and road information. Colors of each sampling site correspond to their census region (Urban regions: Apia Urban Area (AUA) and North West Upolu (NWU), and rural regions: Rest of Upolu (ROU) and Savai'i (SAV)), and the black lines represent the major roads.

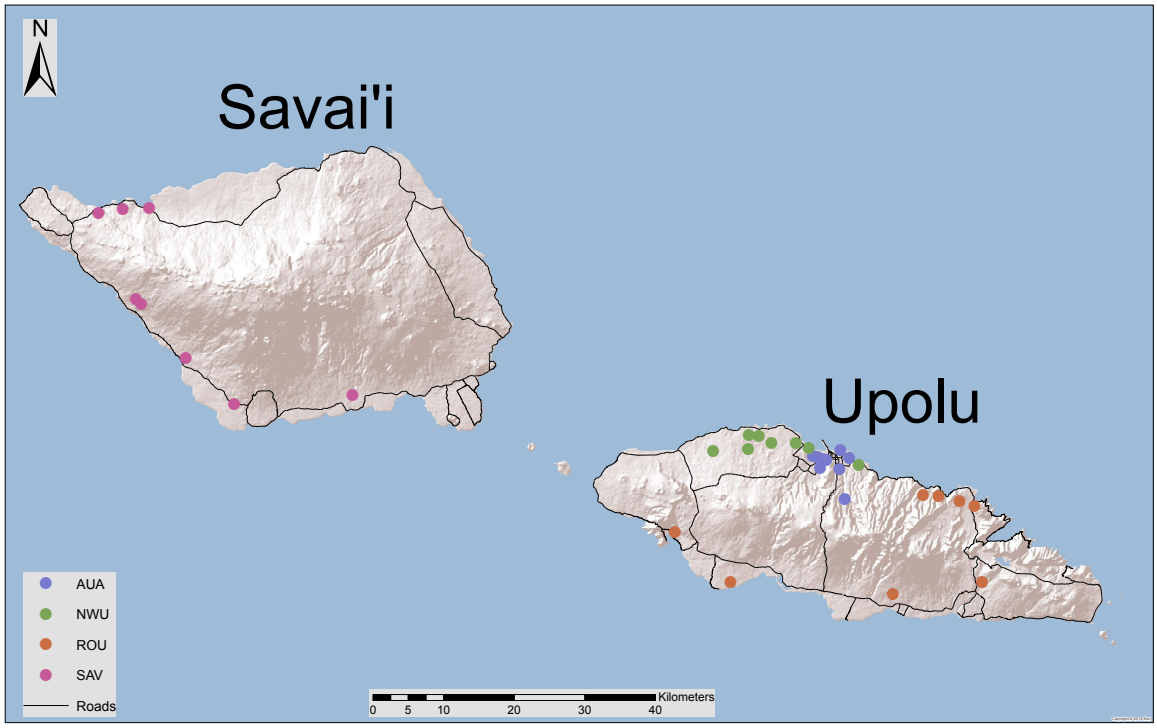


Figure S3. Samoans are closely related to East Asian and Oceanic populations. Three dimensional PCA that displays PC1 on the X axis, PC2 on the Y axis, and PC3 on the Z axis. Samoans are represented by black points. OCE represents Oceanic samples, AMR represents Native American samples, EAS represents East Asian samples, CAS represents Central Asian/Siberian samples, SAS represents South Asian samples, EUR represents European samples, AFR represents African samples, MID represents Middle Eastern samples, and CAU represents Caucusus samples.

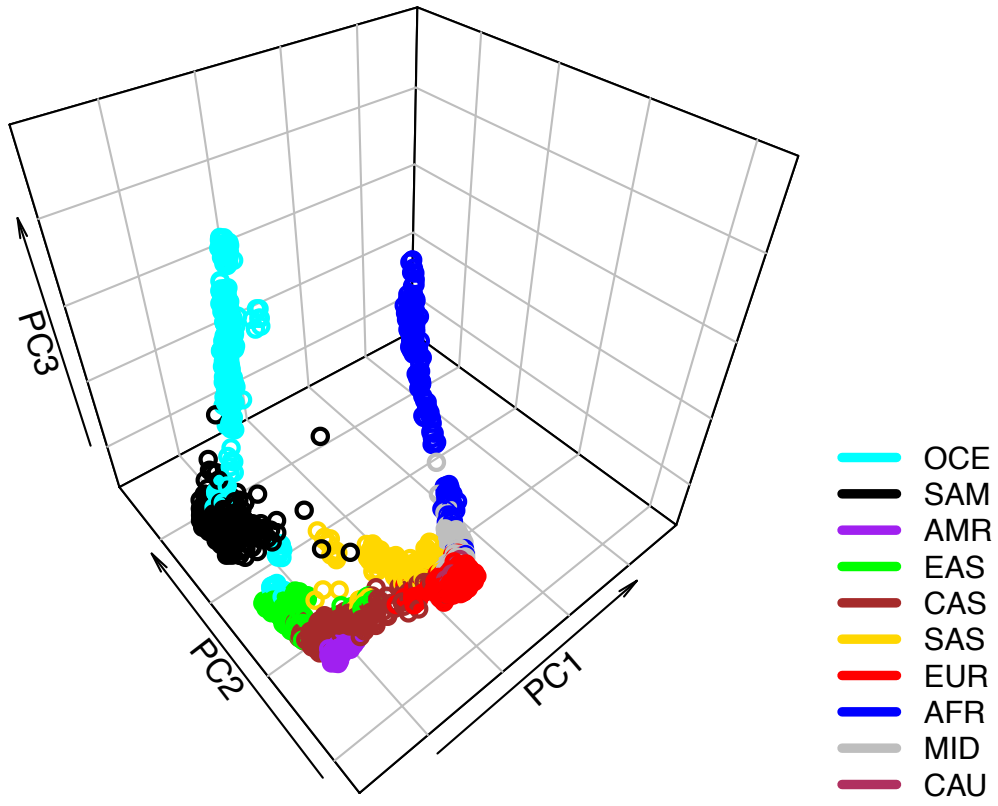


Figure S4. Samoans are most closely related to Tongans within Oceania. PC1 (X axis) and PC2 (Y axis) from a PCA projection of Samoans with at least 99% of their genome attributed to the Austronesian ADMIXTURE cluster (Figure 1A).

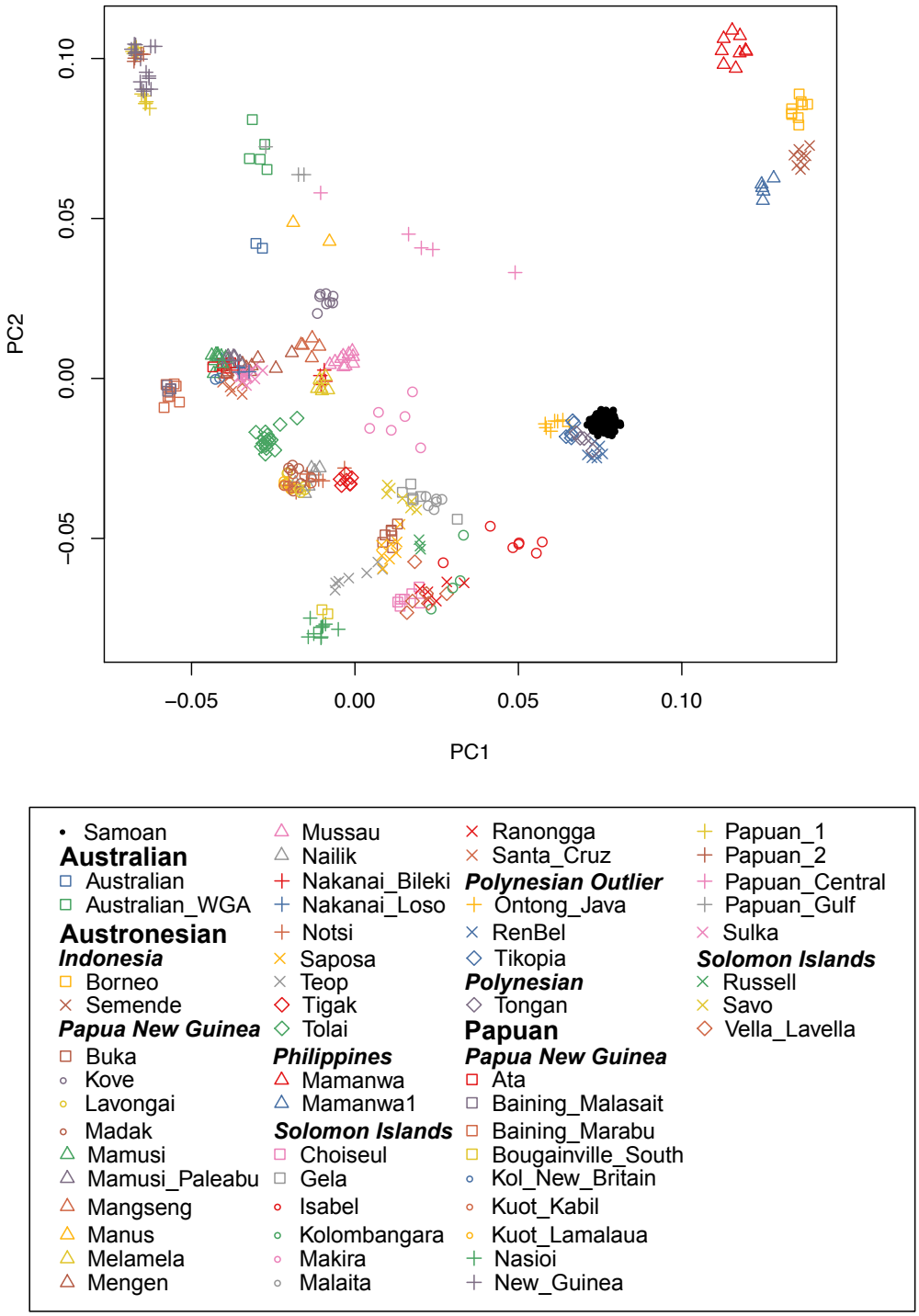


Figure S5. ADMIXTURE sample reference populations. Here we present one example population representative of each major geographic region from the entire merged dataset (see STAR Methods). From right to left: African, European, South Asian, Native American, Central Asian/Siberian, East Asian, Papuan, and Austronesian. Each bar represents one individual and the colors correspond to each ancestral cluster, whose interpretation is below the plot. The magnitude of each cluster is the proportion of each individuals' genome attributed to that cluster.

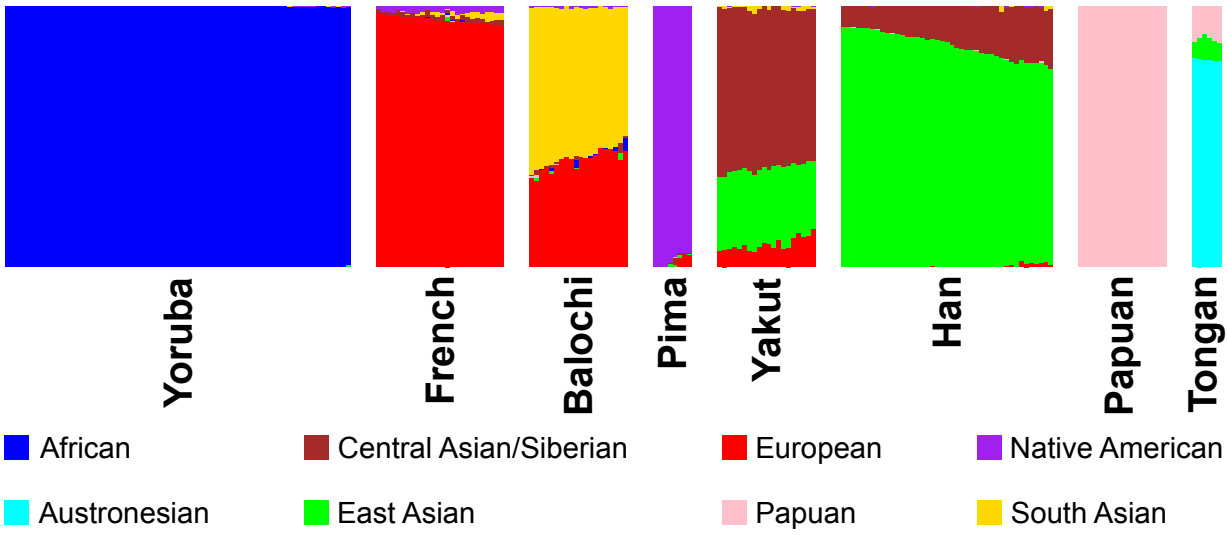


Figure S6. Weak population structure between islands identified through PCA. PC1 and PC2 of all individuals with at least 99% of their genome attributed to the Austronesian ADMIXTURE cluster (Figure 2A). Colors correspond to the individuals' census region. P-values are those that were ≤ 0.05 from an ANOVA Tukey post-hoc analysis. The Cohen's d estimated effect sizes for SAV-AUA, SAV-NWU, and SAV-ROU comparisons along PC1 are 0.7168478, 0.7463582, and 0.8502464 respectively.

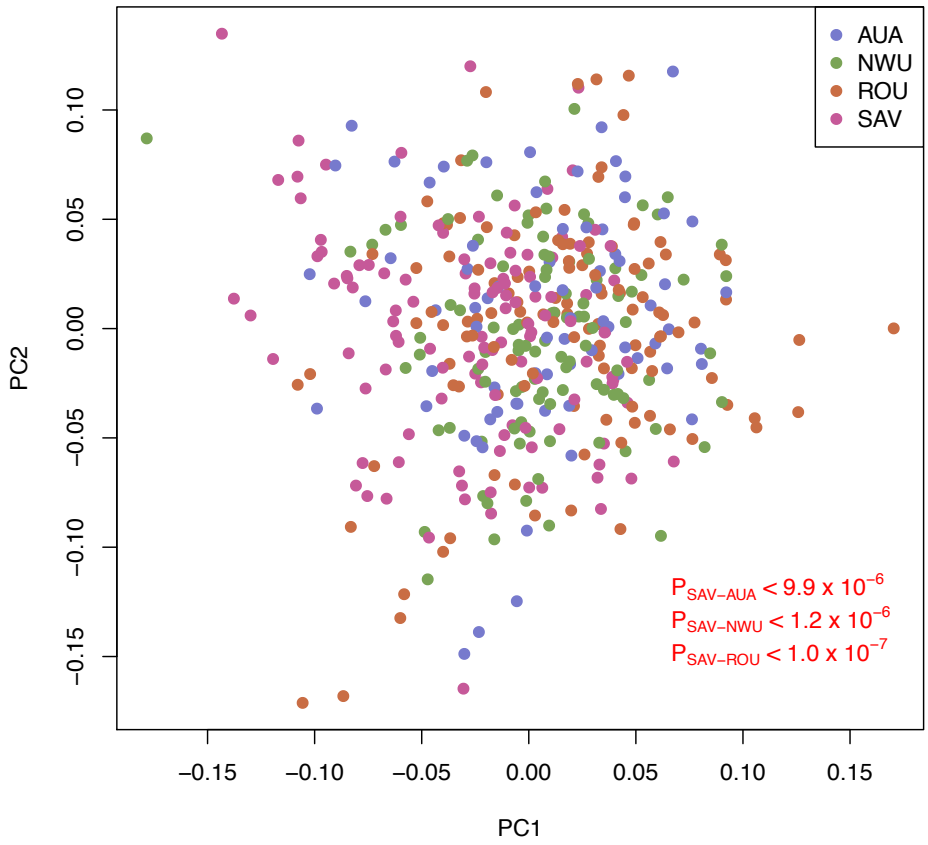


Figure S7. Strong population structure between islands identified with rare variants. Heatmap of the average Jaccard index (29) of F2 variant sharing within and between islands of all individuals with at least 99% of their genome attributed to the Austronesian ADMIXTURE cluster (Figure 2A). All values in the heatmap were multiplied by 10,000 for visualization.

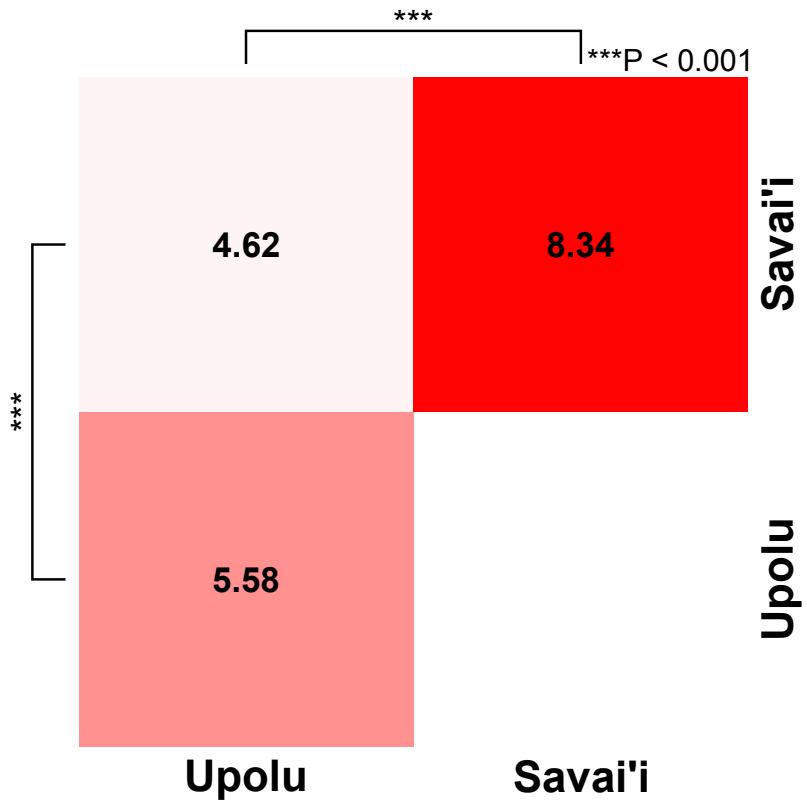


Figure S8 Census region heatmap representation of rare variant sharing (left) and IBD segment sharing (right) with brackets that represents the pair of values whose difference has a P < 0.05 calculated through permutations of census region labels. Rare variant sharing p-values < 0.05 pertain to the following tests: ROU sharing with AUA and SAV, ROU sharing with AUA and NWU, and SAV sharing with AUA and ROU. IBD segment sharing p-values < 0.05 only pertain to ROU sharing with AUA and SAV.

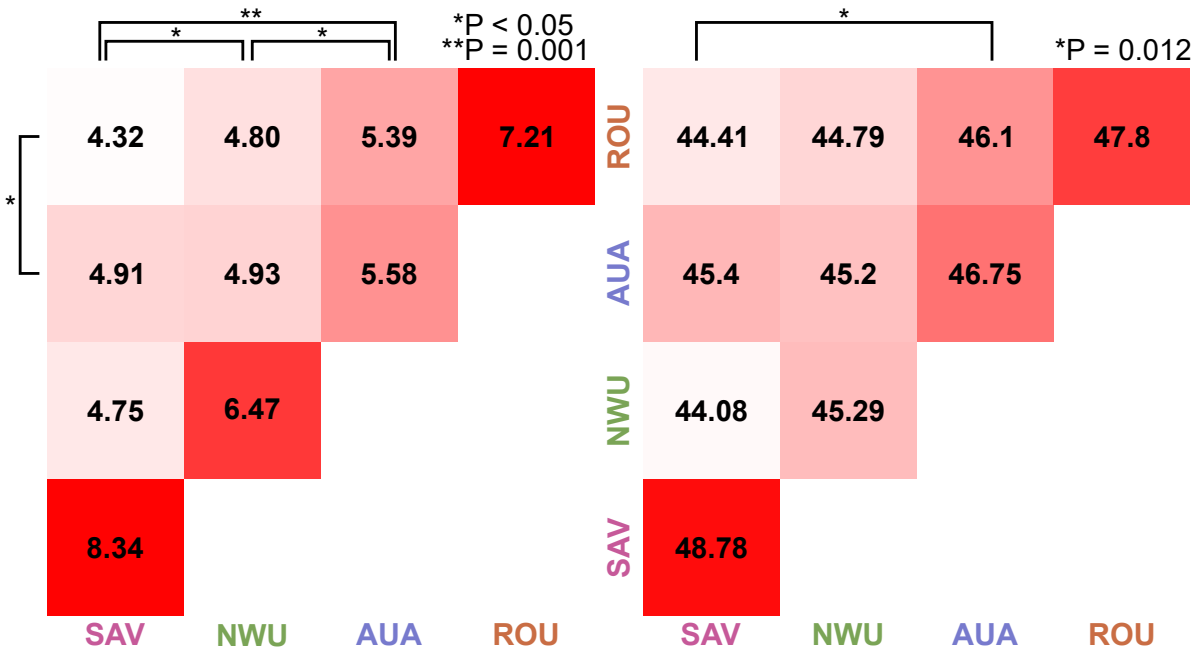
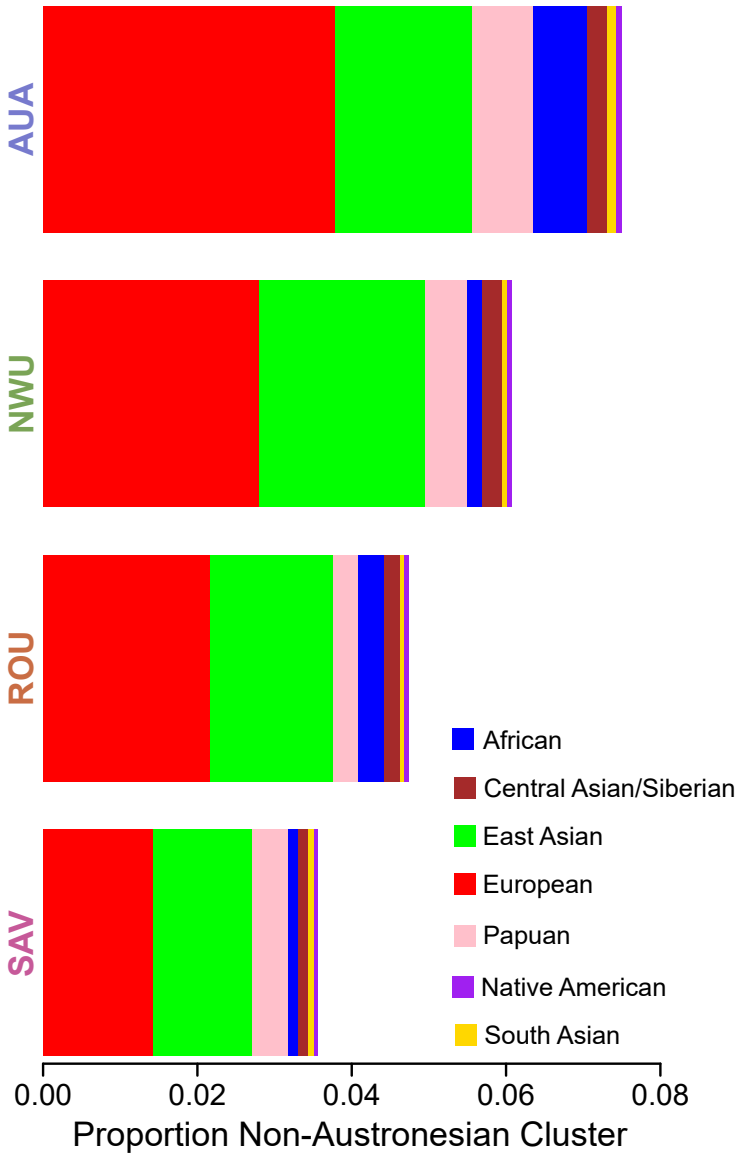


Figure S9. Average non-Samoan cluster ADMIXTURE (30, 31) proportions for each Samoan census region.



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Trans-Omics for Precision Medicine (TOPMed) Consortium Banner Authors

Abe, Namiko	New York Genome Center
Abecasis, Gonçalo	University of Michigan
Albert, Christine	Brigham & Women's Hospital, Cedars Sinai
Almasy, Laura	Children's Hospital of Philadelphia, University of Pennsylvania
Alonso, Alvaro	Emory University
Ament, Seth	University of Maryland
Anderson, Peter	University of Washington
Anugu, Pramod	University of Mississippi
Applebaum-Bowden, Deborah	National Institutes of Health
Arking, Dan	Johns Hopkins University
Arnett, Donna K	University of Kentucky
Ashley-Koch, Allison	Duke University
Aslibekyan, Stella	University of Alabama
Assimes, Tim	Stanford University
Auer, Paul	University of Wisconsin Milwaukee
Avramopoulos, Dimitrios	Johns Hopkins University
Barnard, John	Cleveland Clinic
Barnes, Kathleen	University of Colorado at Denver
Barr, R. Graham	Columbia University
Barron-Casella, Emily	Johns Hopkins University
Beaty, Terri	Johns Hopkins University
Becker, Diane	Johns Hopkins University
Becker, Lewis	Johns Hopkins University
Beer, Rebecca	National Heart, Lung, and Blood Institute, National Institutes of Health

Begum, Ferdouse	Johns Hopkins University
Beitelshees, Amber	University of Maryland
Benjamin, Emelia	Boston University, Massachusetts General Hospital
Bezerra, Marcos	Fundação de Hematologia e Hemoterapia de Pernambuco - Hemope
Bielak, Larry	University of Michigan
Bis, Joshua	University of Washington
Blackwell, Thomas	University of Michigan
Blangero, John	University of Texas Rio Grande Valley School of Medicine
Boerwinkle, Eric	University of Texas Health at Houston
Bowden, Donald W.	Wake Forest Baptist Health
Bowler, Russell	National Jewish Health
Brody, Jennifer	University of Washington
Broeckel, Ulrich	Medical College of Wisconsin
Broome, Jai	University of Washington
Bunting, Karen	New York Genome Center
Burchard, Esteban	University of California, San Francisco
Buth, Erin	University of Washington
Cade, Brian	Brigham & Women's Hospital
Cardwell, Jonathan	University of Colorado at Denver
Carty, Cara	Women's Health Initiative
Casaburi, Richard	University of California, Los Angeles
Casella, James	Johns Hopkins University
Chaffin, Mark	Broad Institute
Chang, Christy	University of Maryland
Chasman, Daniel	Brigham & Women's Hospital

Chavan, Sameer	University of Colorado at Denver
Chen, Bo-Juen	New York Genome Center
Chen, Wei-Min	University of Virginia
Chen, Yii-Der Ida	Lundquist Institute
Cho, Michael	Brigham & Women's Hospital
Choi, Seung Hoan	Broad Institute
Chuang, Lee-Ming	National Taiwan University
Chung, Mina	Cleveland Clinic
Conomos, Matthew P.	University of Washington
Cornell, Elaine	University of Vermont
Correa, Adolfo	University of Mississippi
Crandall, Carolyn	University of California, Los Angeles
Crapo, James	National Jewish Health
Cupples, L. Adrienne	Boston University
Curran, Joanne	University of Texas Rio Grande Valley School of Medicine
Curtis, Jeffrey	University of Michigan
Custer, Brian	Vitalant Research Institute
Damcott, Coleen	University of Maryland
Darbar, Dawood	University of Illinois at Chicago
Das, Sayantan	University of Michigan
David, Sean	University of Chicago
Davis, Colleen	University of Washington
Daya, Michelle	University of Colorado at Denver
de Andrade, Mariza	Mayo Clinic
DeBaun, Michael	Vanderbilt University
Deka, Ranjan	University of Cincinnati

DeMeo, Dawn	Brigham & Women's Hospital
Devine, Scott	University of Maryland
Do, Ron	Icahn School of Medicine at Mount Sinai
Duan, Qing	University of North Carolina
Duggirala, Ravi	University of Texas Rio Grande Valley School of Medicine
Durda, Jon Peter	University of Vermont
Dutcher, Susan	Washington University in St Louis
Eaton, Charles	Brown University
Ekunwe, Lynette	University of Mississippi
Ellinor, Patrick	Massachusetts General Hospital
Emery, Leslie	University of Washington
Farber, Charles	University of Virginia
Farnam, Leanna	Brigham & Women's Hospital
Fingerlin, Tasha	National Jewish Health
Flickinger, Matthew	University of Michigan
Fornage, Myriam	University of Texas Health at Houston
Franceschini, Nora	University of North Carolina
Fu, Mao	University of Maryland
Fullerton, Stephanie M.	University of Washington
Fulton, Lucinda	Washington University in St Louis
Gabriel, Stacey	Broad Institute
Gan, Weiniu	National Heart, Lung, and Blood Institute, National Institutes of Health
Gao, Yan	University of Mississippi
Gass, Margery	Fred Hutchinson Cancer Research Center
Gelb, Bruce	Icahn School of Medicine at Mount Sinai

Geng, Xiaoqi (Priscilla)	University of Michigan
Germer, Soren	New York Genome Center
Gignoux, Chris	Stanford University
Gladwin, Mark	University of Pittsburgh
Glahn, David	Yale University
Gogarten, Stephanie	University of Washington
Gong, Da-Wei	University of Maryland
Goring, Harald	University of Texas Rio Grande Valley School of Medicine
Gu, C. Charles	Washington University in St Louis
Guan, Yue	University of Maryland
Guo, Xiuqing	Lundquist Institute
Haessler, Jeff	Fred Hutchinson Cancer Research Center, Women's Health Initiative
Hall, Michael	University of Mississippi
Harris, Daniel	University of Maryland
Hawley, Nicola L.	Yale University
He, Jiang	Tulane University
Heavner, Ben	University of Washington
Heckbert, Susan	University of Washington
Hernandez, Ryan	McGill University, University of California, San Francisco
Herrington, David	Wake Forest Baptist Health
Hersh, Craig	Brigham & Women's Hospital
Hidalgo, Bertha	University of Alabama
Hixson, James	University of Texas Health at Houston
Hokanson, John	University of Colorado at Denver
Hong, Elliott	University of Maryland

Hoth, Karin	University of Iowa
Hsiung, Chao (Agnes)	National Health Research Institute Taiwan
Huston, Haley	Blood Works Northwest
Hwu, Chii Min	Taichung Veterans General Hospital Taiwan
Irvin, Marguerite Ryan	University of Alabama
Jackson, Rebecca	Ohio State University Wexner Medical Center
Jain, Deepti	University of Washington
Jaquish, Cashell	National Heart, Lung, and Blood Institute, National Institutes of Health
Jhun, Min A	University of Michigan
Johnsen, Jill	Blood Works Northwest, University of Washington
Johnson, Andrew	National Heart, Lung, and Blood Institute, National Institutes of Health
Johnson, Craig	University of Washington
Johnston, Rich	Emory University
Jones, Kimberly	Johns Hopkins University
Kang, Hyun Min	University of Michigan
Kaplan, Robert	Albert Einstein College of Medicine
Kardia, Sharon	University of Michigan
Kathiresan, Sekar	Broad Institute
Kaufman, Laura	Brigham & Women's Hospital
Kelly, Shannon	Vitalant Research Institute
Kenny, Eimear	Icahn School of Medicine at Mount Sinai
Kessler, Michael	University of Maryland
Khan, Alyna	University of Washington
Kinney, Greg	University of Colorado at Denver
Konkle, Barbara	Blood Works Northwest

Kooperberg, Charles	Fred Hutchinson Cancer Research Center
Kramer, Holly	Loyola University
Krauter, Stephanie	University of Washington
Lange, Christoph	Harvard School of Public Health
Lange, Ethan	University of Colorado at Denver
Lange, Leslie	University of Colorado at Denver
Laurie, Cathy	University of Washington
Laurie, Cecelia	University of Washington
LeBoff, Meryl	Brigham & Women's Hospital
Lee, Jiwon	Brigham & Women's Hospital
Lee, Seunggeun Shawn	University of Michigan
Lee, Wen-Jane	Taichung Veterans General Hospital Taiwan
LeFaive, Jonathon	University of Michigan
Levine, David	University of Washington
Levy, Dan	National Heart, Lung, and Blood Institute, National Institutes of Health
Lewis, Joshua	University of Maryland
Li, Yun	University of North Carolina
Lin, Honghuang	Boston University
Lin, Keng Han	University of Michigan
Lin, Xihong	Harvard School of Public Health
Liu, Simin	Brown University, Women's Health Initiative
Liu, Yongmei	Duke University
Liu, Yu	Stanford University
Loos, Ruth J.F.	Icahn School of Medicine at Mount Sinai
Lubitz, Steven	Massachusetts General Hospital

Lunetta, Kathryn	Boston University
Luo, James	National Heart, Lung, and Blood Institute, National Institutes of Health
Mahaney, Michael	University of Texas Rio Grande Valley School of Medicine
Make, Barry	Johns Hopkins University
Manichaikul, Ani	University of Virginia
Manson, JoAnn	Brigham & Women's Hospital
Margolin, Lauren	Broad Institute
Martin, Lisa	George Washington University
Mathai, Susan	University of Colorado at Denver
Mathias, Rasika	Johns Hopkins University
McArdle, Patrick	University of Maryland
McDonald, Merry-Lynn	University of Alabama
McFarland, Sean	Harvard University
McGarvey, Stephen	Brown University
McHugh, Caitlin	University of Washington
Mei, Hao	University of Mississippi
Meyers, Deborah A	University of Arizona
Mikulla, Julie	National Heart, Lung, and Blood Institute, National Institutes of Health
Min, Nancy	University of Mississippi
Minear, Mollie	National Heart, Lung, and Blood Institute, National Institutes of Health
Minster, Ryan L	University of Pittsburgh
Mitchell, Braxton D.	University of Maryland
Montasser, May E.	University of Maryland
Montgomery, Courtney	Oklahoma Medical Research Foundation

Musani, Solomon	University of Mississippi
Mwasongwe, Stanford	University of Mississippi
Mychaleckyj, Josyf C	University of Virginia
Nadkarni, Girish	Icahn School of Medicine at Mount Sinai
Naik, Rakhi	Johns Hopkins University
Naseri, Take	Ministry of Health, Government of Samoa
Natarajan, Pradeep	Broad Institute, Harvard University, Massachusetts General Hospital
Nekhai, Sergei	Howard University
Nelson, Sarah C.	University of Washington
Nickerson, Deborah	University of Washington
North, Kari	University of North Carolina
O'Connell, Jeff	University of Maryland
O'Connor, Tim	University of Maryland
Ochs-Balcom, Heather	University at Buffalo
Paik, David	Stanford University
Palmer, Nicholette	Wake Forest Baptist Health
Pankow, James	University of Minnesota
Papanicolaou, George	National Heart, Lung, and Blood Institute, National Institutes of Health
Parker, Margaret	Brigham & Women's Hospital
Parsa, Afshin	University of Maryland
Penchev, Sara	National Jewish Health
Peralta, Juan Manuel	University of Texas Rio Grande Valley School of Medicine
Perez, Marco	Stanford University
Perry, James	University of Maryland

Peters, Ulrike	Fred Hutchinson Cancer Research Center, University of Washington
Peyser, Patricia	University of Michigan
Phillips, Lawrence S	Emory University
Phillips, Sam	University of Washington
Pollin, Toni	University of Maryland
Post, Wendy	Johns Hopkins University
Powers Becker, Julia	University of Colorado at Denver
Preethi Boorgula, Meher	University of Colorado at Denver
Preuss, Michael	Icahn School of Medicine at Mount Sinai
Prokopenko, Dmitry	Harvard University
Psaty, Bruce	University of Washington
Qasba, Pankaj	National Heart, Lung, and Blood Institute, National Institutes of Health
Qiao, Dandi	Brigham & Women's Hospital
Qin, Zhaohui	Emory University
Rafaels, Nicholas	University of Colorado at Denver
Raffield, Laura	University of North Carolina
Ramachandran , Vasan S.	Boston University
Rao, D.C.	Washington University in St Louis
Rasmussen-Torvik, Laura	Northwestern University
Ratan, Aakrosh	University of Virginia
Redline, Susan	Brigham & Women's Hospital
Reed, Robert	University of Maryland
Regan, Elizabeth	National Jewish Health
Reiner, Alex	Fred Hutchinson Cancer Research Center, University of Washington

Reupena, Muagututi‘a Sefuiva	Lutia I Puava Ae Mapu I Fagalele
Rice, Ken	University of Washington
Rich, Stephen	University of Virginia
Roden, Dan	Vanderbilt University
Roselli, Carolina	Broad Institute
Rotter, Jerome	Lundquist Institute
Ruczinski, Ingo	Johns Hopkins University
Russell, Pamela	University of Colorado at Denver
Ruuska, Sarah	Blood Works Northwest
Ryan, Kathleen	University of Maryland
Sabino, Ester Cerdeira	Universidade de Sao Paulo
Sakornsakolpat, Phuwanat	Brigham & Women's Hospital
Saleheen, Danish	Columbia University
Salimi, Shabnam	University of Maryland
Salzberg, Steven	Johns Hopkins University
Sandow, Kevin	Lundquist Institute
Sankaran, Vijay G.	Broad Institute, Harvard University
Scheller, Christopher	University of Michigan
Schmidt, Ellen	University of Michigan
Schwander, Karen	Washington University in St Louis
Schwartz, David	University of Colorado at Denver
Sciurba, Frank	University of Pittsburgh
Seidman, Christine	Harvard Medical School
Seidman, Jonathan	Harvard Medical School
Sheehan, Vivien	Baylor College of Medicine

Shetty, Amol	University of Maryland
Shetty, Aniket	University of Colorado at Denver
Sheu, Wayne Hui-Heng	Taichung Veterans General Hospital Taiwan
Shoemaker, M. Benjamin	Vanderbilt University
Silver, Brian	UMass Memorial Medical Center
Silverman, Edwin	Brigham & Women's Hospital
Smith, Jennifer	University of Michigan
Smith, Josh	University of Washington
Smith, Nicholas	University of Washington
Smith, Tanja	New York Genome Center
Smoller, Sylvia	Albert Einstein College of Medicine
Snively, Beverly	Wake Forest Baptist Health
Sofer, Tamar	Brigham & Women's Hospital
Sotoodehnia, Nona	University of Washington
Stilp, Adrienne	University of Washington
Streeten, Elizabeth	University of Maryland
Su, Jessica Lasky	Brigham & Women's Hospital
Sung, Yun Ju	Washington University in St Louis
Sylvia, Jody	Brigham & Women's Hospital
Szpiro, Adam	University of Washington
Sztalryd, Carole	University of Maryland
Taliun, Daniel	University of Michigan
Tang, Hua	Stanford University
Taub, Margaret	Johns Hopkins University
Taylor, Kent D.	Lundquist Institute
Taylor, Simeon	University of Maryland

Telen, Marilyn	Duke University
Thornton, Timothy A.	University of Washington
Tinker, Lesley	Women's Health Initiative
Tirschwell, David	University of Washington
Tiwari, Hemant	University of Alabama
Tracy, Russell	University of Vermont
Tsai, Michael	University of Minnesota
Vaidya, Dhananjay	Johns Hopkins University
VandeHaar, Peter	University of Michigan
Vrieze, Scott	University of Colorado at Boulder, University of Minnesota
Walker, Tarik	University of Colorado at Denver
Wallace, Robert	University of Iowa
Walts, Avram	University of Colorado at Denver
Wan, Emily	Brigham & Women's Hospital
Wang, Fei Fei	University of Washington
Wang, Heming	Brigham & Women's Hospital, Partners.org
Watson, Karol	University of California, Los Angeles
Weeks, Daniel E.	University of Pittsburgh
Weir, Bruce	University of Washington
Weiss, Scott	Brigham & Women's Hospital
Weng, Lu-Chen	Massachusetts General Hospital
Willer, Cristen	University of Michigan
Williams, Kayleen	University of Washington
Williams, L. Keoki	Henry Ford Health System
Wilson, Carla	Brigham & Women's Hospital
Wilson, James	Beth Israel Deaconess Medical Center

Wong, Quenna	University of Washington
Xu, Huichun	University of Maryland
Yanek, Lisa	Johns Hopkins University
Yang, Ivana	University of Colorado at Denver
Yang, Rongze	University of Maryland
Zaghloul, Norann	University of Maryland
Zekavat, Maryam	Broad Institute
Zhang, Yingze	University of Pittsburgh
Zhao, Snow Xueyan	National Jewish Health
Zhao, Wei	University of Michigan
Zhi, Degui	University of Texas Health at Houston
Zhou, Xiang	University of Michigan
Zhu, Xiaofeng	Case Western Reserve University
Zody, Michael	New York Genome Center
Zoellner, Sebastian	University of Michigan

TOPMed Population Genetics Working Group

Beame, David

Bowers, Michael

Browning, Sharon

Challagundla, Lavanya

P., Matthew

Daya, Michelle

de, Mariza

Deka, Ranjan

Do, Ron

Francioli, Laurent

Gao, Yan

Gazal, Steven

Gogarten, Stephanie

Gutierrez-Arcelus, Maria

Hall, Ira

Harris, Daniel

Harris, Kelley

Hartman, Kevin

Hernandez, Ryan

Hodonsky, Chani

Raman, Kruthika

Jain, Deepti

Jiang, Jicai

Johnson, Andrew

Johnston, Rich

Jordan, Daniel

Justice, Anne

Min, Hyun

Keely, Addison

Kelly, Tanika

Kessler, Michael

Laurie, Cathy

Liu, Xiaoming

Loesch, Douglas

Luo, Yang

MacArthur, Daniel

Manichaikul, Ani

Mathias, Rasika

McHugh, Caitlin

Mikulla, Julie

L, Ryan

C, Josyf

Nassir, Rami

C., Sarah

Nickerson, Deborah

O'Connell, Jeff

O'Connor, Tim

Page, Grier

Papanicolaou, George

Price, Alkes

Prokopenko, Dmitry

Anne, Jennifer

Raychaudhuri, Soumya

Rotter, Jerome

Schoech, Armin

Schrider, Daniel

Seplyarskiy, Vladimir

Shetty, Amol

Sofer, Tamar

Sohail, Mashaal

Song, Wei

Sotoodehnia, Nona

Spear, Melissa

Sullivan, Patrick

R, Shamil

Szpiech, Zachary

Tang, Hua

D., Kent

A., Timothy

Tiwari, Hemant

Tong, Dominic

Torres, Raul

Vaidya, Dhananjay

Verbanck, Marie

Wehr, Kate

Weir, Bruce

Wong, Quenna

Yanek, Lisa

Yang, Qiong

Zhi, Degui

Zody, Michael

Zoellner, Sebastian